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Microdistributions of stoneflies of the High Tatra montane streams

Abstract: Stonefly samples were collected from disturbed and undisturbed tributaries of the Tatra Mountains streams (the West Carpathians). In the autumn, at stable low discharge, the total density of stoneflies was significantly higher in the undisturbed streams. Microhabitats such as macrolithal (boulders), mesolithal (stones) and moss had higher stonefly density. Taxa of different species or genera have different demands for microhabitats. Very narrow spatial niches were found for the genera *Rhabdiopteryx, Protonemura* and *Perlodes*. The spatial niche overlap was low between the genera *Rhabdiopteryx* and *Brachyptera,* but was high between species of the *Protonemura* and *Leucra* genera. The highest biodiversity of stoneflies was on coarser substrata (except boulders) and moss, the lowest biodiversity was on the finer substrata. Among the organic substrata, a significantly lower coefficient of stonefly α-diversity variation was recorded in mosses compared to submerged wood and roots.

Keywords: microdistribution, running waters, Carpathians, High Tatra Mountains

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1 Introduction

Riparian land use changes the stream habitat structure with consequent effects on aquatic invertebrates [1]. In association with altered catchment hydrology and land cover, inputs of inorganic nutrients from terrestrial sources may interact with increased light availability and stream temperature [2,3]. Catchment land cover has been identified as a major large-scale factor affecting stonefly community composition in streams [4], whereas important medium- and small-scale factors can include stream size, substratum and water quality.

A windstorm in November 2004 flattened 12,000 hectares of forest along southerly oriented slopes of the Tatra Mountains, and also sections of brook catchment areas. Since this windstorm caused large scale destruction of mature forests over such an extensive area, including that of the riverine landscape of the brooks, this unique natural disturbance provided a great opportunity for ecological research [5,6].

The Plecoptera are one of the best bioindicators of human disturbances in streams [7]. Within the benthic macroinvertebrates, stoneflies are selected for evaluation of long-term changes [8]. Stoneflies are useful biological indicators of river quality, reflecting stream degradation, land use, and deforestation [9,10].

Ambühl [11] and Egglishaw [12] relate the distribution of several macroinvertebrate species to current water velocity and substrata. Egglishaw [12] showed that, even in what was apparently a fairly uniform stretch of riffle, i.e. a length of short shallow coarse-bedded stream, the densities of several benthic species varied greatly by site and were correlated with the substrata type. The riverbed gave ground for the interactive linkages between the fluvial-morphological, hydrological-hydraulic and sedimentation processes in space (lateral, longitudinal and vertical dimensions) and in time [13,14]. The result is a dynamic structure of morphological units (microhabitats), which form the basis of the structure and organization of biotic associations. The effects of flow on organisms can be expressed by the complex variable, shear stress [15]. Also, a correlation between average current velocity and hydraulic conditions near the substrate has been described [16], which indicates that average velocity has a significant relationship to conditions on the substratum and biota. Substrate heterogeneity is created by disturbance and variability in physical conditions [17]. Heterogeneity produces patchiness in environmental conditions [18], including food availability, which in turn results in high species diversity in benthic invertebrates.

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Current velocity and substrate characteristics represent the dominant driver of benthic community structures in riverine habitats [19]. The presence and allocation of most organisms are determined by the different velocity and the existence of many hydraulic micro-environments in flowing waters. Substrate texture differences and composition play the main role in controlling benthic coenoses [20].

The availability of trophic resources, such as submerged macrophytes [21], leaf packs or coarse particulate organic matter (CPOM) and organic detritus, controls the stream invertebrate distribution in a considerable way [22]. The annual positive correlation between CPOM and density, biomass and diversity of stoneflies is known. CPOM is important in community structure and function of stoneflies as it provides both food and habitat [23]. It is known that the physical characteristics of the substrate and the presence of other species (e.g. predators) influence the stoneflies selection of microhabitat [24].

Hydraulic and substrate conditions, including the percentage of fine sediment, substrate homogeneity, CPOM and FPOM (i.e. fine particulate organic matter) were determined as the major environmental gradients in habitat and the distribution of invertebrates was significantly correlated with these variables. A probable mechanism affecting the spatial distribution of macroinvertebrates is considered to be hydraulic stress associated with foraging and maintaining position [25].

The stonefly body is adapted to a range of aquatic conditions, and these organisms occupy a diverse range of microhabitats. However, general preferences of most stonefly species are not well known.

Several studies dedicated to the stonefly communities of the High Tatra Mountain rivers revealed a strong influence of environmental factors on larval growth and production of stoneflies in undisturbed and deforested streams. The water temperature appeared as one of the most important environmental factors [6,26-28].

Microdistribution patterns of benthic stream macroinvertebrates are determined by four general environmental variables: substrate particle size, current flow velocity, food substances and other physical/chemical parameters [29]. At the family level, different species of stoneflies showed different substratum preferences [30,31].

This study describes the specific microhabitat requirements of stoneflies and the effect of certain characteristics on stonefly density as well as the response of stoneflies to disturbance due to deforestation. The aim of the present study was to investigate the roles of some riverbed substrata, which potentially affect the spatial niche breadth and niche overlap of stonefly species.

2 Experimental Procedures

2.1 Study area

Fieldwork was undertaken within the Váh and the Poprad catchments in the High Tatra Mountains. The study was carried out in 13 different 3rd and 5th order streams (Fig. 1) in the eco-region of the Carpathian Mountains [28]. Sites 1-6 were in carbonate or semicarbonate basins (calcium range of 7-30 mg/l), while sites 7-13 were in

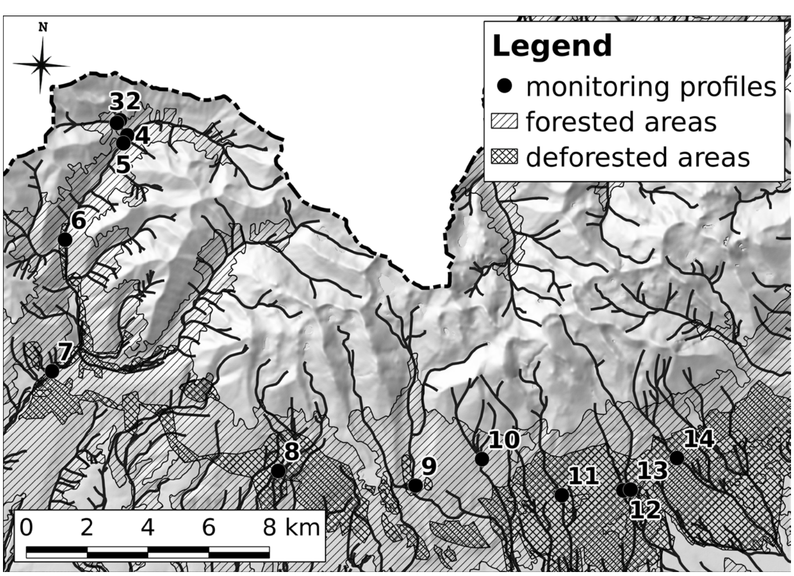

Fig. 1 The drainage area of the studied basins in the High Tatra Mountains and sampling sites.

siliceous basins (calcium range of 3-7 mg/l). The sites had the following characteristics: an altitude range of 944-1333 m a.s.l., a windstorm deforestation range of 0-45.5%, and a Pfankuch-Rosgen channel stability ranking range of 50-133 (Table 1).

2.2 Sampling

Environmental and biological data (Table 1) were collected from 13 sites in March, May, July and October from 2009 to 2011 [32]. Microdistribution and quantitative macroinvertabrate data were collected in early May and late September every year.

Quantitative samples of benthic macroinvertebrates were taken from sampling reaches according to standard AQEM Consortium protocol [33]. Each sample consisted of 20 sampling units taken from different microhabitat types (psammal or sand, microlithal or coarse gravel, mesolithal or stones, macrolithal or boulders, megalithal or large stones, and moss), proportionally according to the presence within a sampling area. A net with 0.3 mm mesh was used and the bottom area of specific substrata was multiplied by the proportion of microhabitat times 25 × 25 cm^2. Thus we sampled approximately 1.25 m^2 stream bottom area. The sampling of the periphyton communities from the substrates was done according to the method described by Punčochář [34]. We removed the periphyton adhering to 7–10 stones using a nylon brush and subsequently we measured the surface area of the stones with aluminium foil. The amount of transported organic matter (TOM) was assessed by taking water samples of 20–25 litres from the stream. Particulate organic matter (CPOM and FPOM) was collected by inserting a sharply pointed cylindrical bottom sampler area = 0.006 m^2) 10–15 cm into the substratum. The material inside the sampler was removed and mixed, by hand, with water. For testing, a subsample of 0.5 litres was taken several times repeatedly for both coarse and fine substrata microhabitats [35]. Particulate organic matter was separated by passing the samples through a nested series of sieves (1.0 mm, 50 µm). Stonefly larvae were identified to the lowest possible taxonomic level, using keys [36-41].

Table 1: Characteristics of the sampled Tatra streams.

Site number	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**
Site name	Tom_1	Tom_2	Jav	Tic_1	Tic_2	Belá	Bie_V	Pop	Vel_Š	Bat	Hro_v	Vel	Sla
Altitude (m)	1292	1186	1300	1172	1057	944	1227	1219	1257	1036	1066	986	1047
Stream order	2	3	2	3	4	5	3	4	3	3	3	3	3
% deforestration	0	0	0	0	3	6.2	37.2	6.4	0	45.5	40.5	28.1	24.1
Stream slope %	15	16.1	20.8	9.9	6.8	5.3	14.3	10.2	31.7	19.3	18.4	15.8	23.1
Channel stability	63	50	51	47	99	58	108	62	62	88	106	133	85
pH*	7.7	8.3	8.1	8	8.1	7.7	7	6.9	7	7	7	7.1	7.2
NO_3 (mg/l)*	2.63	3.1	2.6	1.55	2.65	1.91	2.22	2.25	3.66	3.39	4.86	2.81	2.87
PO_4 (mg/l)*	0.01	0.02	0.02	0.02	0.02	0.01	0.01	0.01	0.02	0.01	0.03	0.01	0.03
Ca (mg/l)*	13.7	30	28.7	13.5	10.2	7.3	7.1	5	3.9	3.3	3.7	4.2	3.6
COD (mg/l)*	7.2	2.5	2.5	4.3	2.5	3.3	4.7	7	11.3	7.1	8.7	4.1	17.8
Psammal %	0	0	0	0	0	0	0	0	5	5	30	5	0
Akal %	0	0	0	5	0	0	5	5	5	0	0	0	0
Microlithal%	5	5	5	50	0	10	5	5	0	5	0	5	5
Mesolithal %	15	10	20	5	50	40	10	35	20	40	25	25	40
Macrolithal %	35	30	30	35	45	35	40	35	25	25	20	25	20
Megalithal %	40	50	40	50	5	15	40	15	40	10	20	35	30
Moss %	5	5	5	0	0	0	0	0	5	15	5	5	5

* arith. mean, COD – Chemical Oxygen Demand

2.3 Data analysis

To test for significant differences among microdistributions of stonefly taxa from different substrata, one-way analysis of variance (ANOVA) and multiple range tests were performed. The spatial niche breadth was calculated according to Sheldon [42]. Niche overlap of spatial resources (microhabitats) was calculated according to Pianka [43].

3 Results

3.1 Stonefly density

Environmental and biotic variables such as periphyton, FPOM, conductivity, nitrogen, coefficient of dispersion (CoD), Pfankuch-Rosgen channel stability and water temperature were related to the change of landscape. On the contrary, dissolved oxygen, CPOM, and fraction of coarse substrata were related to the woodland landscape (Table 1, [32]).

In the autumn, at stable low discharge, the total density of stoneflies was significantly higher in the undisturbed streams (Fig. 2, Table 3). The stonefly density in the undisturbed streams was only slightly higher for individual microhabitats (Table 2) and there were no significant differences within a microhabitat between disturbed and undisturbed streams (Table 3). In both disturbed and undisturbed habitats, the stonefly density

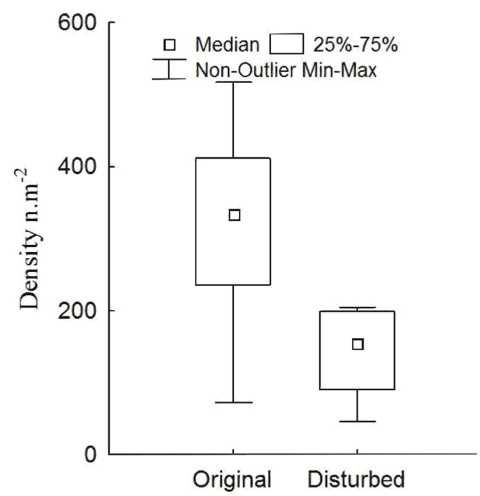

Fig. 2 Box-plots of stonefly density of undisturbed and disturbed streams.

Table 2: Annual mean, spring and autumn stonefly densities in undisturbed and disturbed streams.

Site	Density n.m^{-2}				Total stonefly density of stream n.m^{-2}		
Number*	Microlithal	Macrolithal	Megalithal	Moss	Spring	Autumn	Ann. mean
1	507	505	26	533	346	451	398
2	209	371	59	1151	230	247	239
3	258	447	84	300	145	223	184
4	379	883	185	-	374	336	355
5	-	437	750	-	267	72	170
6	52	240	71	-	567	331	449
8	409	291	36	-	251	517	384
9	185	239	91	308	237	373	303
Mean	**285**	**426**	**162**	**548**	**302**	**319**	**310**
7	122	247	16	76	242	46	144
10	364	287	105	859	186	90	138
11	63	362	141	503	427	204	316
12	379	453	27	844	324	199	262
13	67	116	23	450	495	153	324
Mean	**234**	**302**	**75**	**498**	**308**	**238**	**273**
Total mean	**242**	**379**	**127**	**547**	**301**	**240**	**270**

* Sites 1-9 - undisturbed streams, Sites 7-13 - disturbed streams

Table 3: Variation of stonefly density between microhabitats, habitats, seasons and ecological status of streams.

Psam_Micr$_1$	Meso-Macro$_1$	Mega$_1$	Moss$_1$	Psam_Micr$_2$	Meso-Macro$_2$	Mega$_2$	Moss$_2$
Psam_Micr$_1$	N	N	N	N	N	N	N
	Meso-Macro$_1$	*	**N**	**N**	**N**	**	**N**
		Mega$_1$	*	**N**	**N**	**N**	*
			Moss$_1$	*	**N**	**N**	**N**
				Psam_Micr$_2$	**N**	**N**	**N**
					Meso-Macro$_2$	**N**	**N**
						Mega$_2$	**

	Total density$_1$		Total density$_2$	
	Spring	Autumn	Spring	Autumn
Total density$_1$ spring	N	N	N	*
Total density$_1$ autumn	N	N	N	*
Total density$_2$ spring	N	N	N	*

Key: N > 0.05,* - P < 0.05, ** - P < 0.01; subscript numbers indicate stream type 1 = undisturbed stream, 2 = disturbed streams

increased from megalithal to psamal-microlithal to macrolithal to moss. When the stonefly density between microhabitats was compared there was a significant difference between two microhabitats in only a few pairwise comparisons (Table 3). The microhabitats that were significantly different in stonefly density were meso-macrolithal was greater than megalithal, and moss was greater than psammal-microlithal and megalithal.

3.2 Stonefly microdistribution

Substrata composition influenced the overall abundance of stonefly taxa (Table 4).

Density of some taxa with relatively narrow niche breadth (i.e. *Protonemura intricate, P. montana, P. nimborum, Leuctra autumnalis,* and *Isoperla buresi*) was the highest on moss substrata (Table 4, Fig. 3-6). The density of *Rhabdiopteryx neglecta* and *Leuctra armata* was highest on mesolithal substrata. The density of *Perla grandis* and *Perlodes intricatus* was highest on meso- and macrolithal substrata. Other taxa dominated on microlithal, mesolithal or moss substrata, such as *Leuctra rauscheri*. The genus *Brachyptera* (Fig. 3) avoided fine substrata. *Leuctra pusilla, Leuctra dalmoni,* and *Isoperla sudetica* demonstrated no significant substrate preference and had wide spatial niches (Table 4). Narrow spatial niches were found for the genera *Rhabdiopteryx, Protonemura* and *Perlodes*.

The spatial niche overlap of related stoneflies species is presented in Table 5. The spatial niche overlap was low between the genera *Rhabdiopteryx* and *Brachyptera*, the former preferred mesolithal substrata, the latter preferred various coarse substrata (Table 4).

The spatial niche overlap was high between species of the *Protonemura* genus, excluding *P. intricata*, which preferred finer substrate (Table 4), these were influenced mainly by the phenology of related species (Table 5).

The spatial niche overlap also was high among species of the *Leuctra* genus, excluding *L. dalmoni*, which preferred finer substrata (Table 4), and *L. armata*, which was rare in the moss microhabitat. *Leuctra armata* preferred a microlithal substrate and *L. autumnalis* preferred moss (Fig. 5, Table 4).

A different situation existed among predator habitat preferences, which often had lower spatial overlap. *Isoperla buresi* preferred coarse substrata and moss, while *I. sudetica* was equally distributed. *Perlodes intricatus* and *Perla grandis* were equally distributed but they avoid moss. The last two genera differed by phenology (Table 5) and activity (e.g. growth, feeding). *Perlodes* is especially active in the cold season while *Perla* is active in warmer months [44,45]. Lower stonefly α-diversity was recorded in the microhabitats consisting of psammal, akal and megalithal

Table 4: Spatial niche of stonefly taxa.

Taxa	Spatial Niche mean	Taxa abundance in substrata*
Rhabdiopteryx neglecta	0.14	Psam, Akal, Micro, Macro, Mega, Moss < **Meso**
Brachyptera seticornis	0.54	Psam, Akal, Micro, Moss < **Meso, Macro, Mega**
Protonemura auberti	0.54	Psam, Akal, Micro, Meso, Mega **< Macro, Moss**
Protonemura intricata	0.31	Psam, Akal, Meso, Macro, Mega **< Micro, Moss**
Protonemura nimborum	0.50	Psam, Akal, Micro, Meso, Mega **< Macro, Moss**
Protonemura montana	0.31	Psam, Akal, Micro, Meso,Macro, Mega **< Moss**
Leuctra armata	0.58	Psam, Akal, Macro, Mega, Moss **< Micro, Meso**
Leuctra autumnalis	0.58	Psam, Akal, Micro, Macro, Mega **< Meso, Moss**
Leuctra dalmoni	0.68	No differences
Leuctra pusilla	0.67	No differences
Isoperla buresi	0.53	Psam, Akal, Micro, Mega **< Meso, Macro, Moss**
Isoperla sudetica	0.66	No differences
Perlodes intricatus	0.38	Psam, Akal, Micro, Mega, Moss **< Meso, Macro**
Perla maxima	0.55	Psam, Akal, Mega, Moss **< Micro, Meso, Macro**

Key: bold characters - optimal substrata * compared among substrata by least significant difference test (LSD, α = 0.05)
Psam -psammal, Micro - microlithal, Meso - mesolithal, Micro - macrolithal, Mega - megalithal

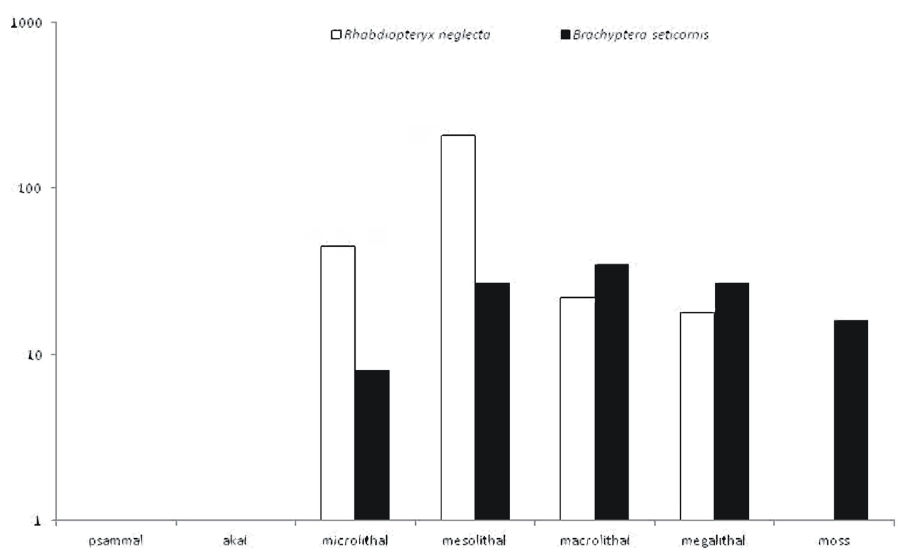

Fig. 3 Microdistribution of Taeniopterygidae.

than in microlithal-macrolithal and organic microhabitats (Fig. 7; F = 10.2, $p < 0.001$, N = 143). Within the organic substrata, mosses, had a significantly lower coefficient of stonefly α-diversity variation than submerged wood or roots, due to a stable water level.

4 Discussion

The windstorm of 2004 in the High Tatra Mountains caused large scale deforestation. The subsequent increase in light availability and stream temperature led to the enhancement of stream primary production resulting in the trophic structure changes of benthic communities. These negative effects on the Tatra stoneflies communities were recorded mainly during the autumn sampling period.

Hydrodynamic models [48] show that the density of stoneflies culminates in the medium-coarse substrates. In the Tatra conditions this would be fully applicable for their biodiversity, but their abundance was bound to the presence of moss substrata.

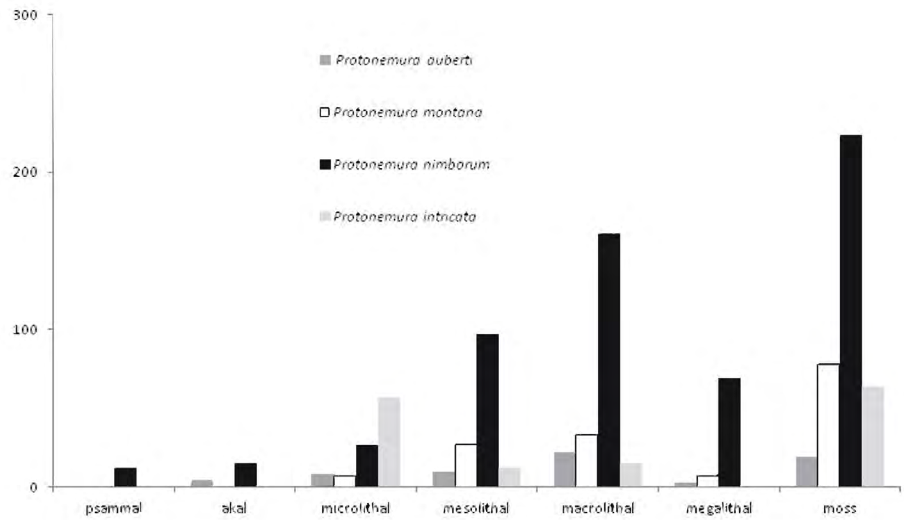

Fig. 4 Microdistribution of Nemouridae

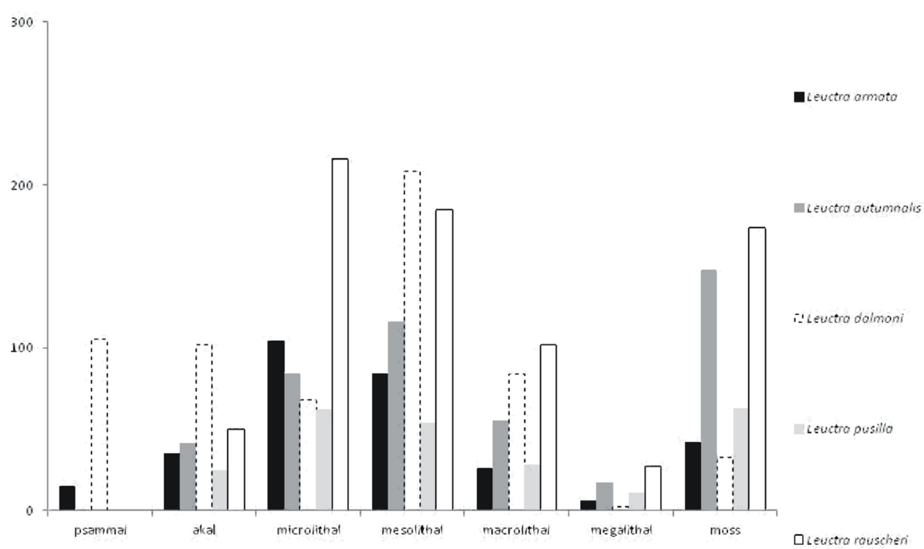

Fig. 5 Microdistribution of Leuctridae.

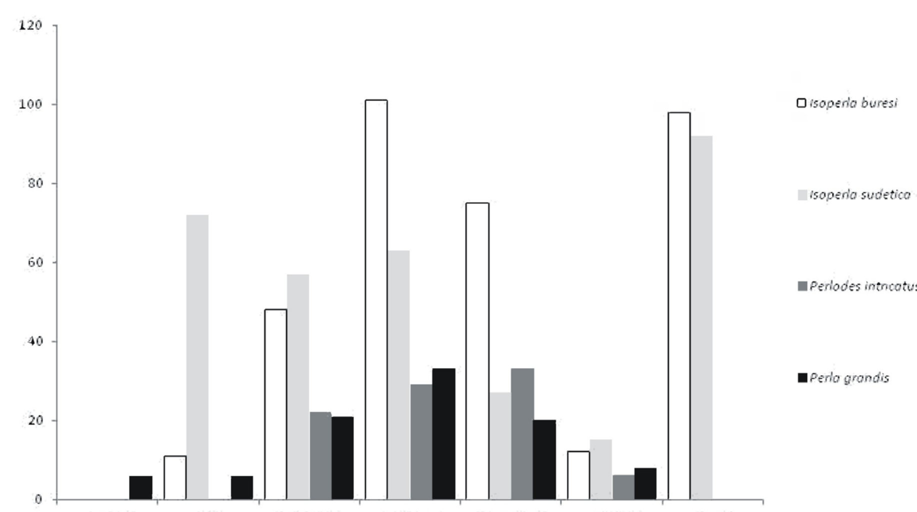

Fig. 6 Microdistribution of Perloidea.

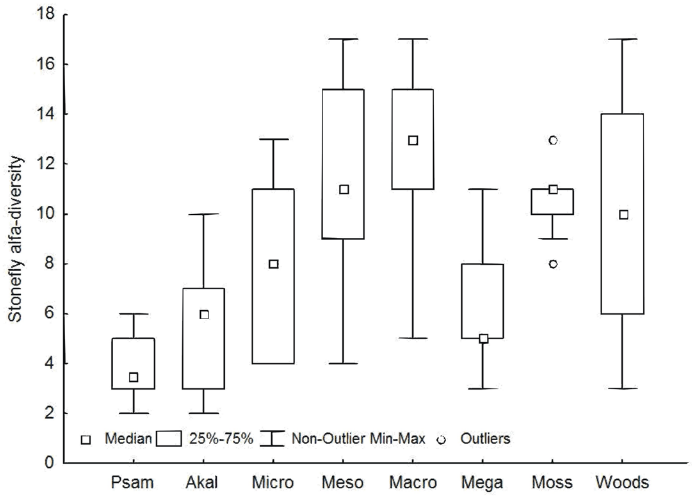

Fig. 7 Box-plots of stonefly α-diversity of microhabitats.

Table 5: The spatial niche overlap of related stonefly species (systematic or ecological).

Species 1	Species 2	Niche overlap*	Generation time and flight period
Rhabdiopteryx neglecta	*Brachyptera seticornis*	**0.61**	Us_2/Us_2
Protonemura montana	*Protonemura nimborum*	0.96	Usu/Us_1
Protonemura montana	*Protonemura auberti*	0.89	Usu/Us_2-su
Protonemura montana	*Protonemura intricata*	0.79	Usu/Us_2
Protonemura nimborum	*Protonemura auberti*	0.95	Us_1/Us_2-su
Protonemura nimborum	*Protonemura intricata*	**0.73**	Us_1/Us_2
Protonemura auberti	*Protonemura intricata*	**0.75**	Us_2-su/Us_2
Leuctra rauscheri	*Leuctra pusilla*	0.99	Us_2/Usu
Leuctra rauscheri	*Leuctra dalmoni*	**0.74**	Us_2/Us_1
Leuctra rauscheri	*Leuctra armata*	0.96	Us_2/Usu
Leuctra rauscheri	*Leuctra autumnalis*	0.96	UJ2/Uje
Leuctra pusilla	*Leuctra dalmoni*	**0.73**	Usu/Us_1
Leuctra pusilla	*Leuctra armata*	0.96	Usu/Usu
Leuctra pusilla	*Leuctra autumnalis*	0.98	Usu/Ua
Leuctra dalmoni	*Leuctra armata*	0.81	Us_1/Ua
Leuctra dalmoni	*Leuctra autumnalis*	**0.72**	Us_1/Ua
Leuctra armata	*Leuctra autumnalis*	0.86	Usu/Ua
Isoperla buresi	*Isoperla sudetica*	0.85	Us_2/Usu
Isoperla buresi	*Perlodes intricatus*	0.79	Us_1/Us_2
Isoperla buresi	*Perla maxima*	0.79	Us_2/S
Isoperla sudetica	*Perlodes intricatus*	**0.56**	Usu/Us_2
Isoperla sudetica	*Perla maxima*	**0.65**	Usu/S
Perlodes intricatus	*Perla maxima*	0.95	Us_2/S

* Calculated according to Pianka [43]; Bold numbers - niche overlap < 0.76; Key: Generation time and flight period according to Krno [38]: U - univoltine, S - semivoltine;
Flight period: s_1 - early spring emerging, s_2 - late spring emerging, su - summer emerging, a - autumn emerging.

Death and Joy [49] found a positive correlation between stonefly abundance and the percentage of forested area. Deforestation of catchments is the main cause of higher frequency of floods, as well as the temperature variations. It also results in a decrease in the frequency of natural wood deposition and debris that leads to lower bottom stability. The subsequent higher portion of biofilms and fine sediments reduce stonefly biodiversity [32,46,47].

In the Ľubochnianka River, the cumulative curve of stonefly distribution on microhabitats of the stream bed, from fine to coarse substrata and moss, had an exponential form (i.e. reflecting an increase in stonefly density on coarse substrata and moss) [10]. The spatial niche breadth of some studied stonefly nymphs taxa was found to be unimodal (Leuctridae, Chloroperlidae, *Perla*), exponential (Taeniopterygidae, Nemouridae), or plateau-shaped (Perlodidae) [50]. The exception from the mentioned pattern was represented by *Isoperla sudetica* (Perlodidae) with the exponential and genus *Rhabdiopteryx* and *Brachyptera* (Taeniopterygidae) with unimodal spatial niche breadth. Substrate type is reaffirmed as a major governing factor in stream macroinvertebrate community structure and dynamics [52]. The species that were strongly associated with one substrate type differed from those associated with another substrate type. According to Egglishaw [12], *Isoperla grammatica* and *Leuctra inermis* were fairly evenly distributed across the width of the stream, but *Perla bipunctata* occurred at greater density in the stream center. *Amphinemura sulcicollis* and *Protonemura* species were abundant in the moss substrata of stony streams, and *Siphonoperla torrentium* was absent from the moss community [12,53,54], as was recorded in the studied rivers. Macrovegetation served as a habitat, with higher abundance of stoneflies linked to macrovegetation presence [55-57]. Hynes [57] also found that all stages of *Isoperla grammatica* occurred in moss in the stony bed of streams. Zwick [58] and Möbes-Hansen, Waringer [59] considered Taeniopterygidae of reophilic taxa bound to boulders and moss, whereas *Nemoura* spp. and *Leuctra* spp. were considered limnophilic-indifferent taxa. At low discharge, *Leuctra inermis* was most abundant at intermediate velocities, but throughout the flumes with the highest density in low velocity areas [60].

According to Pastuchová et al. [61], *Dinocras cephalotes, Taeniopteryx auberti* and *Protonemura praecox* prefered rapids and moss, and *Nemoura uncinata* was rheolimnophilic. *Leuctra hippopus, L. inermis*, and *Perlodes microcephalus* were the most abundant in coarse substrata. Kamler [51] distinguished the Tatra stoneflies into four types, characterizing their different patterns of attachment to the water current speed, which were associated with characteristic substrata: stagnant water species (e.g. *Nemurella pictetii*), slow water current species (e.g. *Protonemura intricata* and *P. austriaca*), slow and moderate current speed species (e.g. *Nemoura uncinata, Amphinemura sulcicollis,* and *Protonemura auberti*) and species that attached over a wide range of water speeds (e.g. *Protonemura nitida, P. montana, Leuctra armata, L. inermis* and *Isoperla sudetica*). In our samples *L. armata* was bound to substrates in a moderate current, *Protonemura nimborum* was bound to coarse substrates and moss with fast current. Microhabitat preferences of the other taxons were consistent with the conclusions of Kamler [51].

A review of microhabitat/substrate preference was provided by Graf et al. [45]. Microhabitat preferences were directly related to the substrate. The categories for this parameter led to 13 microhabitat types, more of them were associated with organic substrate, which played a secondary role, excluding moss, in the Tatra streams. For example, the species *Leuctra inermis* [45] preferred particle organic matter and was uniformly widespread in the inorganic substrates from gravel to macrolithal. A closely related Tatra species *L. rauscheri* favoured micro-mesolithal and moss substrata. *Protonemura montana,* according to Graf et al. [45], was bound only to coarse substrata (meso-macrolithal), whereas the high levels of density of this species in moss were recorded in the Tatra population. The habitat preferences of the Tatra population of *Perla grandis* usually extended well into the finer substrata.

Elliot [62] studied the functional responses of mature larvae of *Perlodes microcephalus*, *Isoperla grammatica*, *Dinocras cephalotes* and *Perla bipunctata* to prey abundance level and their intraspecific interference. Elliot [62] found that interference is applicable to competition between *Dinocras* and *Perla*. *Isoperla* was the least aggressive, and *Perlodes* the most aggressive of the four taxa. *Dinocras* and *Perla* were intermediately aggressive. In our research, we found that the degree of spatial overlap between predators was the lowest among the species *Isoperla sudetica* and the genera *Perlodes* and *Perla*.

In the observed rivers, Eurytopic species and species bound to fine substrata were less sensitive to catchment destruction, in comparison with stenotopic reophilic taxa on coarse substrata and moss. In our samples, related species of the genera *Protonemura, Amphinemura* and *Leuctra* did not show any important differences in microdistribution. However, the differences in macrodistribution (longitudinal zonation) [63] and phenology [64] of these genera are known.

Felmate and Pointing [65] recorded higher substrate colonization positively correlated with higher portion of habitable space in Perlidae nymphs. Apart from this, the surface texture and intersticial flow may influence the habitat preference [66].

The present study analyzed the roles of some riverbed substrata, which potentially affect the spatial niche breadth and niche overlap of stonefly species. The results confirmed high density and biodiversity levels of stoneflies on coarse substrates and mosses when stable hydrological conditions prevail. Very narrow spatial niches were found for the genera *Rhabdiopteryx, Protonemura* and *Perlodes*. The spatial niche overlap was low between the genera *Rhabdiopteryx* and *Brachyptera,* but was high between species of the Nemouridae and Leuctridae. Among the organic substrata, a significantly lower coefficient of stonefly α-diversity variation was recorded in mosses compared to submerged wood and roots.

This study confirmed the specific microhabitat requirements of stonefly species and contributed to the knowledge of microhabitat/substrate preference of European stoneflies [45]. It pointed out on the response of stonefly density to the deforestation.

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